

Effect of ration size on growth and gross conversion efficiency of young lemon sharks, *Negaprion brevirostris*

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Young lemon sharks, *Negaprion brevirostris*, were kept under controlled conditions in an aquarium and fed blue runner, *Caranx crysos*, at different ration levels. The relationship between feeding rate and growth rate was best described by a von Bertalanffy growth curve, which predicted a maximum growth rate of $140 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (0.66% B.W. day^{-1}), a maintenance ration of $199 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (1.06% B.W. day^{-1}), and losses due to starvation of $-236 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (1.11% B.W. day^{-1}). The relationship between gross conversion efficiency (K_1) and feeding rate was also examined. K_1 ranged from -64 to 25% and did not drop at high ration levels. Activity levels of both starved sharks and sharks fed at maintenance were not significantly different (0.2 body lengths s^{-1}). K_1 values generated from both laboratory and field data suggest that young lemon sharks can convert food to new tissue as efficiently as teleosts.

Key words: ration size; growth rates; gross conversion efficiency; lemon shark.

I. INTRODUCTION

Growth is a complex mechanism which represents the outcome of the interactions among several biotic and abiotic factors operating on behavioral and physiological processes. Food intake is the major limiting biotic factor affecting growth in fishes (Brett, 1979). Thus, studying the relationship between growth rate and rate of food intake in fish can be of practical importance for fields such as aquaculture. Likewise, the relationship between food consumed by fish and gross conversion efficiency (K_1) is a necessary foundation to model energy flow between trophic levels in aquatic communities (Warren & Davis, 1967).

Due probably to the difficulty of collecting and keeping sharks in captivity (Gruber, 1980; Gruber & Keyes, 1981), there are no published studies of growth rate v. ration or gross conversion efficiency v. ration relationships for any elasmobranch species.

The purpose of the present study was to evaluate these relationships for young lemon sharks, *Negaprion brevirostris* (Poey) under controlled conditions, as part of a more comprehensive bioenergetic study of the ecology of the lemon shark (Gruber, 1984; Wetherbee *et al.*, 1987; Cortés & Gruber, 1990; Wetherbee & Gruber, 1990; Wetherbee *et al.*, 1990; Cortés & Gruber, 1992).

II. MATERIALS AND METHODS

EXPERIMENTAL PROTOCOL

The lemon sharks were captured on hook and line by fishermen in the Florida Keys (U.S.A.), transported to the laboratory in plastic bags inflated with oxygen and placed in a 6000 l recirculating seawater aquarium divided into two sections (see Gruber, 1980 for details). No more than nine sharks at a time were kept in each section. After a stabilization period of 1 week, each shark was marked by punching holes in the fins. Controls were set at a water temperature of 25° C, air temperature at 25° C, salinity at 30–31 ppt, 12 h D : 12 h L photoperiod, and water depth at 40 cm.

A total of 80 sharks (32 males, 48 females) ranging from 48.0 to 55.7 cm in precaudal length (PCL) were used in eight experimental trials. The groups were based on ration level, which ranged from starvation to maximum voluntary intake.

The experimental food consisted of frozen blue runner, *Caranx crysos* Mitchill. This fish is part of the natural diet of lemon sharks (Cortés & Gruber, 1990) and has been used successfully for many years in feeding experiments (Gruber, 1980).

The food was thawed, cut into boneless fillets, and then 10, 15, 20, 25 and 30 g (wet weight) pieces prepared by weighing on a gram balance. Once a week a multivitamin tablet in a piece of fish was given to each shark. Sharks were fed at about 16.00 hours on Monday, Wednesday and Friday of each week, and each shark's intake was recorded individually. In all experiments there was a control subject in each tank fed *ad libitum*. At the beginning and end of each experiment each shark was weighed, measured (precaudal, fork and total lengths) and sexed. The sharks were allowed 80 h (Wetherbee *et al.*, 1987) to evacuate all the food from the gut and were then weighed.

Energy contents of the food (blue runner) and the shark were determined by adiabatic bomb calorimetry, water content by drying in an oven at 60° C for 72 h to constant weight, and ash content by burning in a muffle furnace at 600° C for 24 h.

Activity rates of starved and fed sharks were monitored randomly at different times of the day and night by timing individuals swimming over a measured 1-m course in the aquarium, to determine whether the starved sharks maintained the same activity level as the sharks kept at maintenance. Activity was measured starting immediately after the sharks were placed under the starvation (8 days) or maintenance (28 days) regimes and throughout the length of these trials.

DATA ANALYSIS

Specific growth rate for each shark was expressed as average daily increase in weight (G_R) calculated using the formula:

$$G_R = (10^{1/n(\log w_n - \log w_o)} - 1) / 100 \quad (1)$$

where w_n is weight at time t , w_o is initial weight, and n is the duration in days between weighings (Winberg, 1956). Gross conversion efficiency was calculated as total growth (in kJ)/total food consumed (in kJ) for each shark.

The relationship between feeding rate and growth rate, and between feeding rate and gross conversion efficiency (K_1) was studied using the results of the eight experiments. The food required for a subject to maintain its weight (maintenance ration), the maximum unrestricted, or *ad libitum*, ration level, the maximum growth rate and the weight losses due to starvation were also established.

III. RESULTS

CALORIC ANALYSIS OF THE FOOD AND SUBJECT

Water, ash, and energy content of the food and experimental subject are given in Table I. The values of water and energy content of the food were in good agreement (within 3%) with values reported by Gruber (1984).

TABLE I. Water, ash, and energy content of the food (*Caranx crysos*) and experimental subject (*Negaprion brevirostris*)

	<i>C. crysos</i>	<i>N. brevirostris</i>
% Water	72.2* \pm 0.9 (74)†	70.6* \pm 0.8
% Ash	4.6 \pm 0.5	10.9 \pm 0.1
kcal g ⁻¹ wet weight	1.365 \pm 0.023 (1.253)	1.294 \pm 0.008
kJ g ⁻¹ wet weight	5.711 \pm 0.096 (5.242)	5.414 \pm 0.033
kcal g ⁻¹ dry weight	4.910 \pm 0.085 (4.819)	4.401 \pm 0.029
kJ g ⁻¹ dry weight	20.543 \pm 0.355 (20.162)	18.414 \pm 0.121
kcal g ⁻¹ ash-free dry weight	5.136 \pm 0.089	4.881 \pm 0.032
kJ g ⁻¹ ash-free dry weight	21.488 \pm 0.372	20.421 \pm 0.134

Values shown are means \pm 1 S.D., based on six replicates.

*This study.

†Values in parentheses are from Gruber (1984).

GROWTH RATES

The amount of food consumed and the amount of substance gained or lost by each shark after the experimental period was expressed as a percentage of the initial wet weight of the shark per day, and in kJ kg⁻¹ day⁻¹ (Table II). A von Bertalanffy growth function (VBGF) of the following form was fitted to the data on daily growth rates *v.* daily feeding rates:

$$G_R = G_{\max} (1 - e^{-k(R - R_{\text{maint}})}) \quad (2)$$

where G_{\max} is maximum growth rate, k is rate of increase in growth rate with increasing feeding rate, R is feeding rate, and R_{maint} is maintenance ration (Fig. 1). This equation was fitted by computer (IBM, Statgraphics Version 2.6) to generate the smallest sum of squares using a non-linear iterative model fitting. G_{starv} , the instantaneous weight loss in the absence of food, was calculated from the fitted equation. G_{starv} and R_{maint} were in fairly good agreement (within 5%) when expressed as a percentage of B.W. day⁻¹ (1.11 and 1.06%, respectively). However, when expressed in kJ kg⁻¹ day⁻¹, they differed by 18%. Based on previous results by Gruber (1984) in which daily loss of body substance during starvation was found to almost match (a 4% difference) daily intake of food during maintenance, we hypothesized that $G_{\text{starv}} = -R_{\text{maint}}$, to obtain a second equation with only two parameters and compare its fit to that of equation (2). Substituting G_{starv} for G_R in the VBGF and solving for k yields:

$$k = \frac{\log \left(1 + \frac{R_{\text{maint}}}{G_{\max}} \right)}{R_{\text{maint}}} \quad (3)$$

When this value of k is substituted in the VBGF the following equation is obtained:

$$G_R = G_{\max} [1 - (G_{\max}/G_{\max} + R_{\text{maint}})^{(R - R_{\text{maint}}/R_{\text{maint}})}] \quad (4)$$

TABLE II. Summary of trials conducted to determine the effect of feeding rate on growth rate and gross conversion efficiency (K_1) of young *Negaprion brevirostris* fed *Caranx crysos* at 25°C

L_{pri} (days)	n (M/F)	PCL (cm)	Initial mean B.W. (g)	Final mean B.W. (g)	X_{food} (g)	Feeding rate*		Growth rate*		K_1 (%)
						A	B	A	B	
8	6/4	54.8 ± 7.0	1963 ± 785	1798 ± 741	0	0	0	-1.12 ± 0.40	-238.5 ± 88.0	—
21	4/5	54.1 ± 4.2	1974 ± 476	1814 ± 569	246 ± 72	0.60	113	-0.34 ± 0.18	-71.1 ± 38.0	-64.0 ± 33.4
28	3/10	53.9 ± 4.3	1981 ± 635	2005 ± 647	632 ± 203	1.14	215	0.04 ± 0.15	16.5 ± 36.4	4.6 ± 15.5
24	4/6	54.5 ± 2.6	2088 ± 283	2174 ± 335	685 ± 138	1.34	252	0.16 ± 0.20	35.1 ± 36.3	13.7 ± 16.5
24	1/2	48.0 ± 0.3	1393 ± 47	1447 ± 46	482 ± 17	1.43	272	0.19 ± 0.19	41.8 ± 41.8	15.2 ± 16.0
21	10/7	55.7 ± 4.9	2083 ± 596	2182 ± 630	708 ± 184	1.56	293	0.21 ± 0.11	45.5 ± 24.6	15.5 ± 8.2
21	1/10	51.7 ± 2.7	1527 ± 142	1629 ± 162	696 ± 84	2.16	406	0.31 ± 0.21	75.3 ± 29.3	18.5 ± 6.8
24	3/4	53.6 ± 2.2	1827 ± 313	2157 ± 431	1230 ± 238	2.73	510	0.61 ± 0.20	129.7 ± 37.6	25.2 ± 7.6

L_{pri} , Length of trial; PCL, precaudal length; X_{food} , mean amount of food consumed. Values are means ± 1 s.d.
*A represents % B.W. per day, B represents $\text{kJ kg}^{-1} \text{ day}^{-1}$.

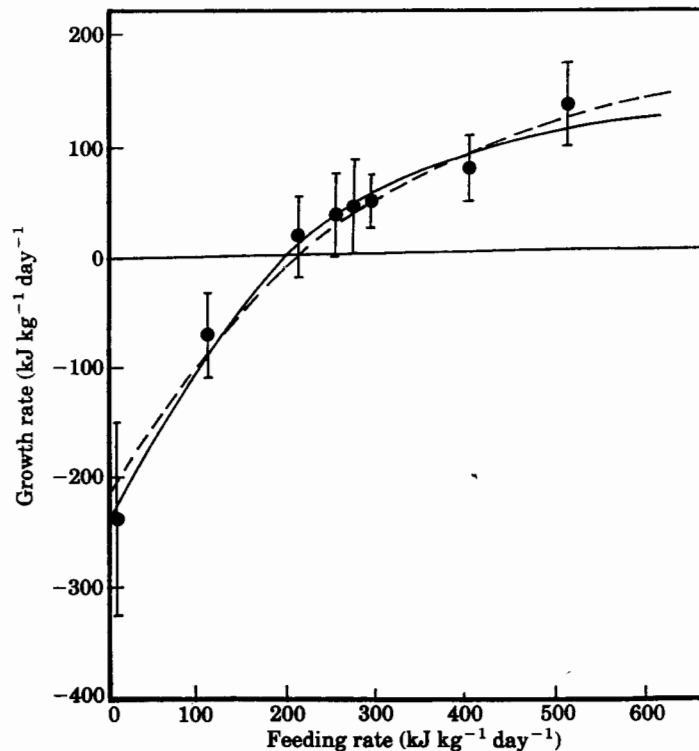


FIG. 1. Growth rates ($\text{kJ kg}^{-1} \text{ day}^{-1}$) for young *Negaprion brevirostris* at 25°C as a function of feeding rates ($\text{kJ kg}^{-1} \text{ day}^{-1}$). (a) von Bertalanffy growth function fitted to the data [equation (2) in text]. (b) Function fitted to the data after fixing $G_{\text{starv}} = -R_{\text{maint}}$ [equation (4) in text]. Values shown are experimental means ± 1 s.d.

This two-parameter model was fitted to data on daily feeding rates v. daily growth rates (equation 4, Fig. 1) using the non-linear iterative procedure described above to generate the smallest sum of squares. The parameters obtained through the two equations are presented in Table III. The coefficient of variation (C.V.) of the residuals (Somerton, 1980) expressed as:

$$\text{C.V.} = \sqrt{(\text{RSS}/N - K)/\bar{Y}} \quad (5)$$

where RSS is the residual sum of squares, N is the number of data values, K is the number of parameters in the model, and \bar{Y} is the mean of the dependent variable (growth rate) was chosen as a measure of goodness of fit because it is adjusted for the number of parameters in each model and the magnitude of the dependent variable. A smaller value of C.V. indicates a better fit. Equation (2) (0.1730) gave a slightly better fit to the data than equation (4) (0.1767).

ACTIVITY LEVELS

Fifty activity measurements were performed for each of six starved sharks and eight sharks fed at maintenance, totalling 700 observations. The pooled results indicated that activity levels did not vary significantly between starved (0.217

TABLE III. Maximum growth rate (G_{\max}), maintenance ration (R_{maint}), instantaneous weight loss during starvation (G_{starv}), all in $\text{kJ kg}^{-1} \text{ day}^{-1}$, and rate of increase in growth rate with increasing feeding rate (k) obtained by non-linear least squares fit of equations (2) and (4) to the growth data for young *Negaprion brevirostris*, also shown are the R^2 and the coefficient of variation of the residuals (C.V.)

Parameters	Equation (2)	Equation (4)
G_{\max}	140.021	177.305
k	0.0049	—
R_{maint}	199.367	213.494
G_{starv}	-236.081	
R^2	0.855	0.847
C.V.	0.1730	0.1767

body lengths $\text{s}^{-1} \pm 0.196 \text{ s.d.}$) and fed sharks ($0.209 \text{ body lengths s}^{-1} \pm 0.134 \text{ s.d.}$) (ANOVA; $F=0.854$, $P>0.05$, $n=14$).

CONVERSION EFFICIENCY

The relationship between gross conversion efficiency (K_1) and daily feeding rate (Fig. 2) shows more scatter than the growth v. ration curve because K_1 contains the combined errors of both the growth and feeding estimates. The K_1 v. ration curve rises steeply towards R_{maint} , where by definition $K_1=0$, then continues to rise at a much slower rate. However, it does not reach an asymptote or show a drop in conversion efficiency at high ration levels. The maximum experimental conversion efficiency, given by G_{\max}/R_{\max} , was 25.2% (Table II).

IV. DISCUSSION

Several important parameters can be derived graphically from the curve describing the relationship between growth rate and ration. The 'typical' GR curve (Brett, 1979) starts at zero ration (R_0) with a negative growth rate (G_{starv}) and rises steeply to cross the point of zero growth (G_0) at the maintenance ration (R_{maint}). Then the steep slope of the curve progressively decreases to an asymptote corresponding to the maximum growth rate (G_{\max}) and the maximum ration (R_{\max}). The optimum ration (R_{opt}) is obtained by tracing a tangent from the origin to the point of maximum slope in the curve (Arunachalam & Reddy, 1981; Pandian, 1982). The value of the von Bertalanffy growth function we used is that it incorporates some of these important parameters (G_{\max} , R_{maint}) or permits derivation of the others (G_{starv} , R_{\max}). However, the asymptotic segment of the GR curve was not detected in this study because the maximum growth rate of $140 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (0.66% B.W. day^{-1}) predicted by the VBGF would only be attained at a feeding rate of about $1200 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (6.4% B.W. day^{-1}), whereas the maximum voluntary feeding rate obtained for sharks under the experimental conditions was only $510 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (2.73% B.W. day^{-1}), resulting in a G_{\max} of $130 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (0.61% B.W. day^{-1} ; Table II). The occurrence of linear or nearly linear relationships between growth and feeding

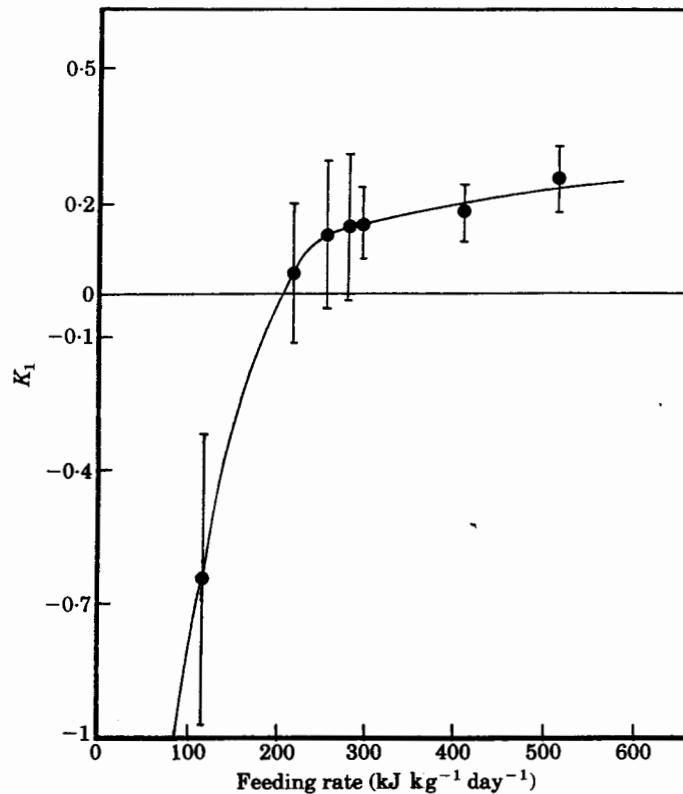


FIG. 2. Gross conversion efficiencies for young *Negaprion brevirostris* at 25°C as a function of feeding rates (kJ kg⁻¹ day⁻¹). Values shown are experimental means \pm 1 s.d. The best fitting curve was traced by eye.

rates is nevertheless not uncommon in young fish (Davies & Massey, 1977; Borgman & Ralph, 1985; Klaoudatos & Apostolopoulos, 1986).

Making $G_{\text{starv}} = -R_{\text{maint}}$ did not improve the fit to the data, since equation (2) (three-parameter model) still fitted the data better than the new two-parameter model thus obtained [equation (4)]. The rationale behind this hypothesis can be illustrated with the help of the energy equation [Winberg (1956)]: $C = G + M + FU$, where C is consumption, G is growth, M is metabolism, and FU represents excretory and faecal losses. At the maintenance ration ($G=0$), the input of food consumed equals the output as metabolism and excretion plus faeces. During starvation ($C=0$), the amount of substance lost ($-G$) equals the metabolic requirements plus the excretory and faecal losses. Assuming that the energy lost in excretory products and faeces (FU) remains the same during starvation and maintenance, and that activity is the main factor affecting metabolic rate, then if activity does not differ between starvation and maintenance, the maintenance ration must equal the body substance lost. While we found that activity remained similar during an 8-day starvation period and a 4-week maintenance ration regime, further research is needed to determine the extent of excretory and faecal losses, and metabolic rates during starvation and maintenance to test whether indeed $G_{\text{starv}} = -R_{\text{maint}}$.

Food supply is the primary factor affecting growth in fish (Brett, 1979), but other abiotic and biotic factors may affect growth directly, or indirectly by acting upon feeding and metabolism, and thus upon the conversion of food into new tissue. Important environmental factors, such as temperature, salinity, and light conditions were kept constant, thereby eliminating confounding effects and variability of these factors on feeding and growth rates. Ammonia content and pH of the water did not vary throughout and among experimental trials, and dissolved oxygen was kept at saturation by bubbling air into the tank water. In general, water quality was maintained by recirculation through a mechanical and a biological filter, and by replacing the water in the aquarium monthly (see Gruber & Keyes, 1981 for details on the aquarium system).

Among the biological factors that may affect the relationship between ration and growth at a given temperature, are age, size, and metabolic rate of the fish (Paloheimo & Dickie, 1965; Huisman, 1976), specific dynamic action (SDA; Kausch, 1968), absorption and assimilation efficiency (Averett, 1969), and level of activity (Kerr, 1971). In the present study differences in age and body size of the experimental sharks were kept small in an effort to minimize possible effects of these variables.

A decrease in gross conversion efficiency with larger rations found by several investigators (Paloheimo & Dickie, 1966a,b; Kelso, 1972; Huisman, 1976 among others) has been attributed to an increase in SDA (Pandian, 1967; Kausch, 1968), to a decrease in absorption efficiency and assimilation efficiency, to a decrease in the proportion of the assimilated energy available for growth and an increase in the proportion used for metabolism, and to increased activity of the fish (Kerr, 1971; Brett, 1979). In the present study no decrease in K_1 was observed at high ration levels. This is because we were unable to induce young lemon sharks to feed voluntarily at intake levels high enough to yield lower growth efficiencies. In addition, metabolic rates for lemon sharks fed increasing rations were not available, but activity levels for sharks fed at maintenance and for starved sharks remained relatively constant, suggesting that metabolic requirements did not vary in excess between the two groups.

The values of K_1 we obtained ranged from -64 (submaintenance ration) to 25% (*ad libitum* ration). At intake levels above maintenance, K_1 ranged from 10 to 25%, which agrees with values reported for most carnivorous teleosts (Brett & Groves, 1979). Using growth rates from the field, as determined from mark and recapture techniques (Gruber & Stout, 1983; Manire & Gruber, 1991) and estimates of daily ration in the wild (Cortés & Gruber, 1990) we estimated that the young lemon shark converts food into new tissue with an efficiency of about 9.5 to 13%. Finally, we used estimates of growth from the field for age-0 and age-1 lemon sharks and plotted them in the laboratory-derived VBGF, which yielded K_1 values ranging from about 10 (age-1) to 12% (age-0). Thus, the estimates of K_1 generated by the VBGF and those calculated on an annual basis from field estimates of growth and consumption are in agreement. The occurrence of higher K_1 values derived from the experiments conducted in the laboratory (Table II) can be explained by the decreased metabolic requirements of sharks kept in captivity. Using available data from the literature we also calculated gross conversion efficiency on an annual basis for age-0 sandbar sharks, *Carcharhinus plumbeus* (Nardo), and for age-0 and age-1 spiny dogfish,

TABLE IV. Estimates of production (P), consumption (C), and gross conversion efficiency (K_1) for young of several shark species, all values expressed on an annual basis

Species	Temperature (°C)	P (g)	C (g)	$K_1 (=P/C)$	Reference
<i>Squalus acanthias</i>					
Age-0	10	37	346	10.7%	Jones & Geen (1977)
Age-1	10	31	508	6.1%	Jones & Geen (1977)
<i>Carcharhinus plumbeus</i>	25	1065	7556	14.1%	Medved <i>et al.</i> (1988)
<i>Negaprion brevirostris</i>	32	1388	10 572*–14 801†	9.4–13.1%	Present study

*Calculated using a daily ration of 1.5% B.W. day⁻¹.†Calculated using a daily ration of 2.1% B.W. day⁻¹.

Squalus acanthias (L.) (Table IV). K_1 for age-0 dogfish (10.7%) is in the lower end of the range of K_1 s for most carnivorous teleosts, but decreases to 6.1% for age-1 sharks. This value seems consistent with the slow growth rates and long digestion time reported for this species at mean temperatures of 10° C (Jones & Geen, 1977). However, K_1 for young sandbar sharks is a little higher than that of young lemon sharks. Since growth rates for young sandbar sharks (Medved *et al.*, 1988) are very similar to those of young lemon sharks (Gruber & Stout, 1983; Manire & Gruber, 1991) the higher daily ration of the lemon shark may account for the difference in gross conversion efficiency between the two species.

Growth in the lemon shark does not appear to be limited by the ability to absorb energy (Wetherbee *et al.*, 1990), or to convert assimilated energy to new tissue. Instead, we believe that the slow rates of growth reported for lemon sharks (Gruber & Stout, 1983; Brown & Gruber 1988; Manire & Gruber, 1991) are the result of a low level of food intake (Cortés & Gruber, 1990) and a slow rate of digestion (Cortés & Gruber, 1992).

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